SEASONAL TRENDS IN THE RELATIVE ABUNDANCE OF JAPANESE BEETLE POPULATIONS IN THE SOIL DURING THE ANNUAL LIFE CYCLE

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INTRODUCTION

Since 1927 the Japanese Beetle Laboratory at Moorestown, N. J., has conducted, under the immediate supervision of the writer, several series of field surveys to determine the status of Japanese beetle populations in the soil in various parts of the territory known to be generally infested with the insect. One series, designated the "seasonal series," was, in part, planned to show each year the seasonal trends in abundance during the course of the annual developmental cycle of the insect; and another series, called the "periodic series," was designed to show the major changes in population occurring from one year to the next. Only the results obtained in the first series are considered in this paper. However, since these surveys were confined to the section close to the original point of entry of the Japanese beetle into this country, and therefore long subject to infestation, data from a third series of surveys, conducted since 1932 in Salem County, N. J., in cooperation with the New Jersey Department of Agriculture, are also included to show to what extent the same trends hold in more recently infested territory.

LIFE CYCLE OF THE JAPANESE BEETLE

In its present main distribution area, the developmental cycle of the Japanese beetle begins in the summer of one year with the deposition of eggs in the ground by the adult beetles of one generation and terminates in the summer of the suceeding year with the emergence from the ground of the adult beetles of the next generation. There is thus but one generation a year.

In the vicinity of Philadelphia egg deposition extends from the middle or last of June until well along in October, but the number of eggs laid after September 1 is insignificant compared with the number deposited during July and August. Under the usual summer conditions in this area the eggs hatch in from 2 to 3 weeks, and the resulting larvæ grow rapidly, all but a small proportion attaining their full size by the middle of September. The relatively small number of larvæ hatched late in the season grow more slowly because of the lower temperatures, and hence do not become more than half grown before the oncoming of winter precludes any further growth until the following spring. Such retarded larvæ reach their full growth late in May, when the more advanced larvæ are beginning to pupate. The pupæ normally appear about June 1 and are the dominant stage in the soil during much of that month. Under normal temperatures for that time of year, the pupal stage lasts from 10 to 15 days, and shortly after its appearance the adult beetle works its way up through the soil to the surface of the ground and thence either crawls or flies to near-by vegetation, upon which it begins to feed. In the area under consideration the first adult beetles usually appear above ground between June 10 and 20, though ordinarily they do not become abundant until about July 1.

EXPECTED TRENDS IN POPULATION AS JUDGED FROM LIFE HISTORY

From the foregoing it is evident that during the summer all stages of the Japanese beetle are present in the soil, but at other seasons, roughly from September 15 until June 1 of the succeeding year, the population is composed almost or quite exclusively of larvæ, most of which are in the last, or third, larval instar.

Since all but a negligible proportion of the eggs are deposited in the summer, there can be no increase in the insect's population in the soil during the remainder of the annual cycle. Consequently, unless mortality during the summer has been exceptionally heavy, it is to be expected that each year a Japanese beetle population will attain its greatest abundance early in September and that all subsequent changes in numbers will be in the nature of a decrease.

SEASONAL SERIES OF SURVEYS

Method of Making a Survey

In view of the known habitat preferences of Japanese beetle larvæ, which form the predominant stage in the soil-inhabiting populations of the insect, the surveys have been conducted for the most part in permanent grasslands, such as pastures and the "roughs" of golf courses. In such sites it was expected that soil and vegetational conditions would probably remain nearly uniform, thereby making it possible to relate observed changes in population directly to influences associated with the passage of time.

At each point of examination a layer of sod 1 foot square was removed, and the larvæ and other soil-inhabiting stages found in the underlying soil were collected and counted. Several diggings were made over a stated period, and the average number of individuals per digging was then computed. This figure served as an index of the relative abundance of the insect at that point during the period in question.

During the first years of these surveys the examinations of the soil at each station were confined to a small tract of grassy sod, so that any consequent injury to the land, which was privately owned, would be as inconspicuous as possible. It was found, however, that some of the results obtained under such circumstances were far from representative of the general neighborhood, and it thus became necessary at times to shift the site of the examinations. These changes made it questionable how far the results obtained at different times were comparable with one another. To remedy this situation, and since in the meanwhile experience had shown that any sod injury due to the diggings was only temporary, late in 1929 the surveys were extended over much larger areas at nearly all the stations.

Compilation of Data

Since this paper is concerned solely with the more general trends in the changes in abundance of Japanese beetle populations occurring during an average single annual life cycle, no attempt is made to describe these features as observed in any specific year. Instead, the results of all, or a fair proportion of, the years for which records are available are combined for each period into a single average, which therefore serves as an index of the relative abundance of the insect during that period. The results, as given in table 1 and figure 1, *A,* have been summarized from records of beetle abundance covering 7 consecutive years in a group of 8 stations, 4 in New Jersey and 4 in an adjoining section of Pennsylvania, all situated within 12 miles of the beetle's original point of entry into this country. Since, as implied in the preceding paragraph, the surveys during the first 3 years were conducted under less nearly uniform conditions than those conducted later, the results based upon the last 4 years are listed separately in table 1, and graphically shown in figure 1, *B,* to show how far they substantiate the indications afforded by the full series of records.

In this series of surveys the individual records obtained at each station were summarized each year for every half-monthly interval for which records were available, throughout the annual life cycle. This procedure gave, for each interval in any 1 year, a series of 8 averages of the number of individuals occurring beneath 1 square foot of sod. The common average of all 8 stations for each interval was then obtained. From these common averages for each year the general averages over a term of years were obtained, which afford a good index of the relative size of the population at any given time of the year. The general results obtained in this way are listed in table 1 under the heading "Average number of individuals per square foot, observed."

Besides giving the observed averages computed from the field records, together with their probable errors, table 1 also lists the averages as estimated by inspection from graphs[1] of seasonal

[1] The graphs were first drawn free-hand and, with the exception of the left-hand ascending portion covering the first summer, were then adjusted by successive approximations until the algebraic sum of the deviations of the estimated from the observed averages so closely approximated zero that the difference was negligible (Ezekiel, Methods of Correlation Analysis, p. 132, 1930). On account of the small size of younger larvæ, which form the predominant stage in the soil during July and August, and the consequent difficulty of finding all of them during an examination of the soil, it is believed that the averages obtained during those months are somewhat lower than those obtained early in the fall; hence the writer feels justified in drawing the graphs of summer abundance through or considerably closer to the higher than

trends based upon the observed averages and the relations, in percentages, that the estimated populations in the different half-monthly periods bear to the maximum average population in the first half of September.

DISCUSSION OF RESULTS

Comparison of the percentages listed in table 1, and also of the graphs in figure 1, for the 7- and 4-year series shows a close general agreement as regards the general direction and extent of change at successive intervals throughout the beetle's life cycle.

Perhaps the most noteworthy feature shown is the practical absence of any decrease in the population during the winter, which is generally regarded as the season of heaviest insect mortality. The records of the individual years of this period are, with few exceptions, consistent in this respect. Even after the abnormally cold winter of 1934, the spring surveys revealed in general a beetle population reduced little, if at all, below that found late in the autumn of 1933.[2] Winter therefore seems to have a conserving effect on a Japanese beetle population, tending to maintain it at the general level that it had reached late in the autumn when the larvæ entered hibernation.

Reduction in the population is clearly shown to be coincident with the occurrence of warm weather, and, in so far as it is not caused by the emergence of adults from the ground, which in the area involved usually does not begin much before June 15, is suggestive of biotic agencies as the responsible factor. The conserving action of winter may accordingly be attributed to the inhibiting effect of temperature upon the activities of the associated soil organisms, although it may also be due in part to the relative inaccessibility of the larvæ at this season of the year when, because of the depth at which they hibernate, they are

to the lower averages (table 1, fig. 1). As a result the algebraic sum of the deviations of the estimates from the observed values shows a marked negative trend (−4.3 in the 7-year series; −1.1 in the 4-year series). The standard error of the estimates is ± 0.85 in the 7-year series and ± 0.72 in the 4-year series.

[2] Fox, Henry. Some misconceptions regarding the effects of the cold of February, 1934, on the larvæ of the Japanese beetle, *Popillia japonica* Newman. Jour. Econ. Ent., 28: 154–159. 1935.

TABLE 1. SUMMARY OF SEASONAL SURVEYS TO DETERMINE JAPANESE BEETLE POPULATIONS IN THE SOIL AT HALF-MONTHLY INTERVALS THROUGHOUT THE INSECT'S DEVELOPMENTAL CYCLE

Period[1]	Seven-year series (1927–1934)				Four-year series (1930–1934)			
	Number of square feet examined	Average number of individuals per square foot		Per cent of maximum estimate	Number of square feet examined	Average number of individuals per square foot		Per cent of maximum estimate
		Observed	Estimated			Observed	Estimated	
June 16–30	1726	.1 ± .04	.1	.6	1246	.2 ± .08	.2	1.4
July 1–15	1359	3.0 ± .40	3.0	17.8	816	3.9 ± .42	3.8	25.7
16–31	1592	5.9 ± .69	6.9[2]	40.8	1010	6.7 ± .70	7.0[2]	47.3
Aug. 1–15	1383	8.3 ± .96	10.9[2]	64.5	846	9.2 ± 1.23	10.2[2]	68.9
16–31	1469	14.3 ± 1.69	14.9[2]	88.2	845	13.3 ± 2.12	13.4[2]	90.5
Sept. 1–15	1277	16.9 ± 2.00	16.9	100.0	890	14.8 ± 2.63	14.8	100.0
16–30	1342	16.0 ± 1.47	16.0	94.7	913	13.7 ± 2.00	13.7	92.6
Oct. 1–15	1630	14.9 ± 1.18	14.9	88.2	1138	12.2 ± 1.31	12.3	83.1
16–31	1764	12.5 ± .90	13.9	82.2	1223	10.3 ± .68	12.2	82.4
Nov. 1–15	1272	13.6 ± 1.42	13.4	79.3	878	11.7 ± 1.17	12.2	82.4
Mar. 16–31	1138	13.4 ± 1.45	12.9	76.3	601	12.4 ± 2.23	12.0	81.1
Apr. 16–30	1606	13.4 ± 1.21	12.8	75.7	1025	13.0 ± 1.81	11.9	80.4
May 1–15	1688	12.5 ± 1.24	12.5	74.0	1012	13.0 ± 2.14	11.8	79.7
16–31	1834	11.2 ± 1.00	11.4	67.5	1134	11.1 ± 1.51	11.1	75.0
June 1–15	1937	9.6 ± .77	9.6	56.8	1219	9.6 ± 1.26	9.6	64.9
16–30	1785	7.1 ± .68	6.9	40.8	1078	6.7 ± 1.07	6.7	45.3
July 1–15	1401	2.8 ± .54	2.8	16.6	858	2.0 ± .47	2.0	13.5
16–31	1732	.3 ± .11	.3	1.8	1028	.2 ± .03	.2	1.4
Aug. 1–15	1502	.0 ± .01	.0	.0	903	.0 ± .00	.0	.0

[1] The half-monthly periods from June 16 to August 15 are included twice, pertaining in the first place to the early stages in the beetle's developmental cycle, and in the second to the final stages of the same generation when adults are emerging above ground. Records of the periods between November 16 and March 15, and between April 1 and 15 are incomplete.

[2] Graphs of summer populations passing through observed values usually exhibit a pronounced dip or sag in their middle section. Because of the relatively minute size of the earlier larval stages, which predominate during much of the summer, a somewhat larger proportion of them are doubtless missed in the soil examinations than is the case with eggs (conspicuous because of their white color and relative firmness) or older larvæ. It accordingly seems justifiable to estimate the populations between mid-July and late August at a somewhat higher value than is indicated by the observed averages. This correction is especially called for in the 7-year series, the earlier surveys of which during the summers were conducted under rather unfavorable conditions.

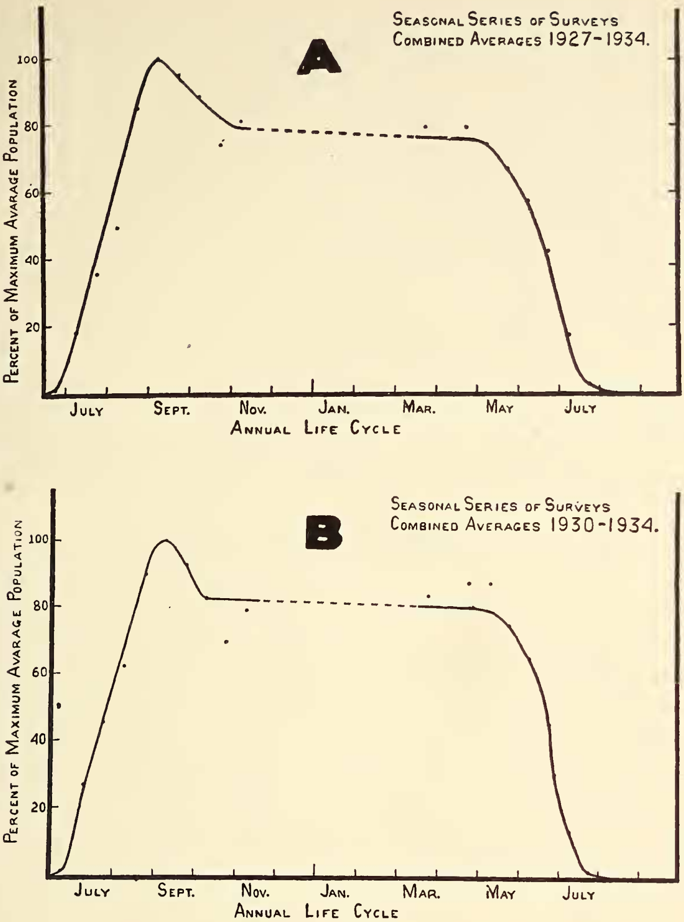

FIGURE 1.—Seasonal trends in the relative abundance of Japanese beetle populations in the soil during the annual life cycle, in percentage of the population for the period September 1–15: *A*, Estimates based upon records of 7 consecutive years (1927–1934) in the seasonal series of surveys; *B*, estimates based upon records of the last 4 (1930–1934) of the 7 consecutive years in the same series of surveys.

largely protected from birds and other animals feeding at the surface.

It is obvious that any mortality in a population during its first summer is normally more than compensated for by the continued deposition and hatching of eggs. Hence, throughout July and August—the 2 months of active egg laying—the population shows a steady net increase until the maximum population is reached early in September. Thereafter, egg deposition having practically ceased, the decreasing trend in the population is no longer obscured. As the graphs show, the decrease continues as long as warm weather lasts in the autumn. When the weather becomes cold this decrease is arrested until early in May of the succeeding year. With the return of warm weather, the decrease is again clearly shown and becomes all the more striking as the temperature rises late in May and early in June. Probably the decrease in the population would be still more rapid with the occurrence of higher temperatures in midsummer, but any decrease at that time due to mortality cannot be distinguished from that resulting from the simultaneous emergence of adult beetles from the ground.

All reductions in population previous to the beginning of adult emergence must be a result of the various destructive agencies to which the insect is exposed in the ground in the course of its life cycle. In table 1 the population during the first half of June is indicated as averaging from 57 (7-year series) to 65 (4-year series) per cent of its maximum abundance the preceding September. It thus appears that a Japanese beetle population suffers a reduction from destructive agencies of from 35 to 43 per cent between the first part of September of one year and the middle of June of the succeeding year. Some of this destruction is doubtless caused by birds and other animals which feed upon the larvæ, but it is the view of the writer that by far the greater part is due to native soil-inhabiting microorganisms (pathogenic bacteria, fungi, protozoa, parasitic nematodes) originally infecting the immature stages of native Scarabæidæ and spreading thence to those of the introduced Japanese beetle.

Thus far there is no clear evidence that the introduced parasites of the Japanese beetle have played more than a minor rôle in bringing about the observed reductions in abundance of the insect. These reductions have been too general and wide spread to be attributable to the introduced parasites, which to date have been mostly confined to small areas in the immediate vicinity of the points of liberation. However, the recent marked increase in their numbers at several of the stations where introductions have been made suggests that in the future these parasites are likely to play a far more important rôle in reducing Japanese beetle populations than they have up to this time. Although the outlook is as yet rather indefinite, developments in the parasite situation, although provokingly slow in reaching a decisive point, have in the past few years taken so promising a turn as to give good ground for optimism in the hope that the introduced parasites will furnish the key to the eventual control of the Japanese beetle. Realization of the potentialities in this direction, however, should not be permitted to blind one to the possibly indispensable, even if minor, rôle likely to be played by the less obtrusive organisms of native origin, which apparently have heretofore been mainly instrumental in effecting at least partial control of Japanese beetle populations.

COOPERATIVE SERIES OF SURVEYS

Since the seasonal series of surveys were confined to the vicinity of the original point of entry of the Japanese beetle into this country, the question naturally arises whether conditions similar to those just described would hold in other portions of its range. Information on this point was supplied from a series of cooperative surveys conducted between 1932 and 1934 in various pastures distributed through a heavily infested portion of Salem County, N. J. This section is situated from 25 to 40 miles from the original center of spread of the insect and did not become generally infested until 1929.

These surveys differed from those of the seasonal series in that they were not always conducted in the same group of stations. Consequently, the conclusions drawn in regard to the seasonal changes in population are based upon a consideration of all the available evidence and not exclusively upon that from any uniform set of pastures.

Inasmuch as no surveys have ever been conducted in Salem County during that part of the summer when egg deposition is most actively in progress, no data were available for charting the course of population change previous to its reaching its maximum abundance early in the autumn (fig. 2). The only surveys made at a time in the year when the population was close to a maximum was a series conducted in 9 pastures from September 20 to 22, 1933. These gave at that time a common average of 14.0 larvæ per square foot. A resurvey of the same pastures from October 6 to 11 of the same year showed a common average of 10.1 larvæ to the square foot, a decrease of 28 per cent (fig. 2).

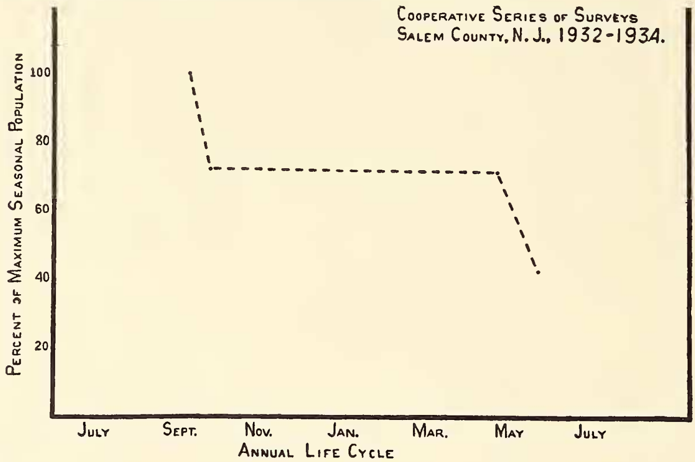

FIGURE 2.—Seasonal trends in relative abundance of Japanese beetle populations in the soil in percentages of the maximum average population in September, based upon records of the cooperative series of surveys for the period 1932–1934 in Salem County, N. J.

Records from a much larger number of pastures made it possible to compare populations found in Salem County during October with those occurring late in April and early in May of the succeeding year. A series of 20 pastures examined between October 18 and 28, 1932, and again between April 25 and May 4, 1933, yielded on the earlier occasion a common average of 11.5 and on the later one of 10.7 larvæ per square foot, a decrease of 7.0 per cent. Another series of 21 pastures (including most of those of the preceding group) examined October 2 to 11, 1933, and April 30 to May 11, 1934, gave for the earlier period a common average of 13.6 and for the later one of 14.6 larvæ per square foot, an increase of 7.4 per cent. The common average, + 0.2 per cent of the two sets of data thus accords fairly well with the evidences of relatively insignificant winter decrease found in the seasonal series of surveys (*cf.* Figs. 1 and 2).

A comparison of the populations of pastures in Salem County early in May with the populations early in June is made possible by records from surveys made in 1933 and 1934. In the former year a series of 5 pastures, which about May 1 had yielded a common average of 22.1 larvæ per square foot, gave from June 5 to 8 an average of 10.5 larvæ and pupæ combined, a decrease in about 1 month of 52.5 per cent, while in 1934 a series of 4 pastures, which early in May had indicated a common average of 17.6, gave from June 4 to 6 an average of 12.4 larvæ per square foot, a decrease of 29.5 per cent. The average decrease from May to June for the 2 years was therefore 41.0 per cent (fig. 2).

By comparing these various results in relation to the maximum average population recorded in September, it is found that in October the decrease was 28 per cent, by the last of April or early in May the population remained essentially unchanged, while by the first part of June 57.5 per cent had been lost. Because they are based upon data from diverse sources, these figures can scarcely be regarded as more than very general approximations, but they show seasonal trends in Japanese beetle populations in the course of the annual life cycle that are in substantial accord with those indicated in the records of the seasonal series of surveys.

SUMMARY

Records of field surveys of the abundance of the soil-inhabiting population of the Japanese beetle conducted throughout the greater part of each year in a group of 8 stations, all situated within 12 miles of the original point of entry of the insect, and covering a total range of 7 consecutive years, reveal certain clearly defined trends in the course of its annual life cycle.

The general trends shown in Japanese beetle populations as regards relative abundance during the annual life cycle are consecutively as follows: (1) A rapid increase beginning late in June and extending through the summer, coincident with the season of active egg deposition, resulting in (2) the population reaching its maximum abundance early in September. This is followed by (3) a brief interval of rapid decrease lasting until

mid-October, (4) a long period of little or no apparent change extending through the winter and until about May 1 of the succeeding year, and (5) a second period of rapid decrease extending through May and into June, when adult emergence begins.

The absence of any significant winter reduction is attributed largely to the inhibitory effect of winter temperatures upon the activities of soil organisms parasitic or predatory upon the larvæ.

Rapid reductions in population are normally coincident with the occurrence of warm weather, and are therefore suggestive of biotic agencies as the cause. After June 15 the reduction is largely conditioned by the appearance of adults and their emergence from the ground, but previous to that date all reductions result from the various destructive agencies to which the immature stages of the insect are exposed in the soil, among which various native soil-dwelling organisms, parasitic or predatory upon the Japanese beetle, appear to play a major rôle, with birds and other surface-feeding animals playing a minor part.

Reductions in populations of the Japanese beetle due to its imported parasites have been too strictly local to figure as a significant factor in bringing about the general seasonal reductions recorded in this paper. More recent developments in the general parasite situation, however, hold much of promise as regards the eventual control of the Japanese beetle by the imported parasites.

The essential features in these changes in relative abundance of Japanese beetle populations throughout the annual cycle, which are primarily indicated in the records of continuous surveys in the older infested sections of the insect's range, are duplicated in the records of other surveys conducted in a more recently infested section in Salem County, N. J.